WHAT DO NEURONAL NETWORK MODELS OF THE MIND INDICATE ABOUT ANIMAL CONSCIOUSNESS?

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The attempt to provide a firm scientific basis for understanding consciousness is now in full swing, with special contributions from two areas. One is experimental: brain imaging is providing ever increasing detail of the brain structures used by humans (and other animals) as they solve a variety of tasks, including those of higher cognition. The other is theoretical: the discipline of neural networks is allowing models of these cognitive processes to be constructed and tested against the available data. In particular, a control framework can be created to give a global view of the brain. The highest cognitive process, that of consciousness, is naturally a target for such experimentation and modelling. This paper reviews available data and related models leading to the central representation, which involves particular brain regions and functional processing. Principles of consciousness, which have great relevance to the question in the title, are thereby deduced. The requisite neuronal systems needed to provide animal experience, and the problem of assessing the quality and quantity of such experience, will then be considered. In conclusion, animal consciousness is seen to exist broadly across those species with the requisite control structures; the level of pain and other sensations depends in an increasingly well-defined manner on the complexity of the cerebral apparatus.

Introduction

Neural networks have progressed enormously over the 50 or so years since they were first introduced. They were based originally on the simplest of possible models of the living brain nerve cell: it is a decision unit, programmed to respond if the total input of electrical charge over its surface (cell body plus dendritic outgrowths) is above a certain level. Otherwise it remains 'silent'. Learning rules for the modification of the strengths of the connections between model neurones (which I will term here simply neurons, to distinguish them from living 'neurones' in the brain) have also been developed, as well as a more general understanding of their powers. It has been demonstrated, for example, that they possess the ability to act as 'universal approximators', being able to approximate, to any level required (by using enough neurons), any specified function from inputs to outputs (Hornik *et al* 1989). The increasing ability to understand what artificial neural networks are able to achieve has led to their growing application throughout industry and commerce. At the same time, we are understanding ever better how they can be used to explain the functional processing of modules of neurones in the brain. Such simplified models are now being employed to explore how higher-level cognitive processes, such as language, action

planning and encoding, and the retrieval of episodic memories can be performed. At the highest cognitive level, they form the foundation for an analysis of consciousness, although with concomitant involvement of neural network models of lower-level processing. These possibilities will be considered later. First we must turn to the facts of life for consciousness before we can appreciate the sort of models we might construct of them. Both human and animal consciousness are relevant areas for such exploration.

The problem of animal consciousness has occupied many and engendered much controversy. Since there is as much, if not more, argument over human consciousness, especially as to its nature, it is understandable that the more difficult problem of animal minds should remain unresolved. A solution to the problem of how the brain creates consciousness for humans will help resolve the question for other animals.

The quest for the neuronal correlates of consciousness (NCC) in the cerebral cortex is now proceeding apace (Taylor 1999). Many attempts have been made to track down the sites which may be necessary for consciousness to be present, and whose neuronal activity is well correlated with conscious experience; a review of progress on this is provided by Taylor (1999). However, there is still uncertainty as to sufficient conditions needing to be observed of neuronal activity for the network of sites involved in the brain to be claimed as *the* sites of consciousness. Here a framework is developed, and related criteria deduced, so that neuronal sites can be selected to give a first approximation of such important areas. This is then applied to some questions of animal consciousness.

The problem we presently face in the search for the NCC is that the nature of consciousness is subtle, and its characteristics seem to change from moment to moment. In order to prevent the NCC from wandering all over the brain, be it now in the primary sensory or unimodal associative cortices (Pollen 1999), or now in the prefrontal cortex (Crick & Koch 1998), we will initially explore evidence in support of various possible sitings of the NCC. We then turn in the section *Characteristics of Consciousness* to consider certain criteria which must be satisfied by neuronal activity for a region to be a candidate for the NCC, and conclude that the inferior parietal lobes are the most appropriate for siting consciousness. In the following section we develop the notion of the central representation, which contains the crucial contents for consciousness, and demonstrate in the next section a neural model possessing the general flow of information in the brain which incorporates the central representation. In the section *Animal Consciousness* we consider how the nature of the central representation can be explored by means of an engineering control approach to attention. The relevance of this for animal consciousness is then developed in the following section, *Animal Welfare Implications*, including a brief consideration of pain experience in animals. A brief discussion concludes the paper.

Experimental data

The data we consider are varied: from single cells; lesion effects on behaviour; and from brain imaging, using especially positron emission tomography and functional magnetic resonance imaging (fMRI). The single cell data involve the presence or absence of significant activity observed in an animal under anaesthesia, which has little effect on early sensory cortical responses (in early visual cortices, for example; Moutoussis & Zeki 1997) nor in inferotemporal cortex (Tanaka 1996). However, there is a considerable effect of anaesthesia on parietal lobe single cell responses, leading to great difficulty in taking measurements from such cells before the advent of the ability to measure awake behaving monkeys (Milner & Goodale 1995).

As a start to considering lesion effects, we note the singular lack of loss of consciousness due to frontal deficits, brought about either by disease or injury. The cases supporting this claim are numerous. For example, there is the famous case of Phineas Gage (Damasio 1995), who had a tamping iron blown through his frontal lobes with considerable loss of frontal cortex but without successive loss of consciousness as he was carried to the local doctor. There is also the case of the young man born without most of his frontal lobes (Damasio 1995), who, although suffering from social problems, lived a conscious existence.

One behavioural effect of brain lesions of particular relevance to the NCC is that of neglect. Patients showing this condition have usually suffered damage to the right parietal lobe, and have subsequently lost awareness, for example of visual input in their left hemifield. This loss, for example, is observed in the inability to cross out lines on the left of their field of view. However, their lot can be ameliorated by vibration of the neck muscles, and in general shows a dependence on body signals. Thus, neglect can be loss of awareness in a body-centred frame of reference (although there may also be object-frame dependence of their loss; Karnath 1997). It is now agreed that neglect arises specifically from damage to the inferior parietal lobe (Milner 1997).

Much is also being discovered about the siting in the cortex of buffer working memories. Those for spatial vision are in the right inferior parietal lobe (Jonides & Smith 1997), those for language and temporal estimation in the left (Coull & Nobre 1998). On the other hand, extinction, involving loss of awareness of the right hand object of two similar objects, one on the left, one of the right, is sited in the superior parietal lobe (Milner 1997).

There are recent fMRI data indicating that there is also the experience of the motion after-effect (MAE) most strongly in the supramarginal gyrus in the inferior parietal lobe. The experimental paradigm to observe this uses motion adaptation to a set of horizontal bars moving vertically downwards for 30s, and then stopping. Subjects exposed to such a display usually experience the MAE for 9 or so seconds after cessation of the movement of the bars (Tootell *et al* 1995).

Whole-head fMRI measurements during this paradigm (Taylor *et al* 2000) show a network of connected areas, as illustrated in Figure 1. This network has a posterior group, involving especially the motion area MT, which was found to be responsive to all forms of motion as well as the MAE (Tootell *et al* 1995). On the other hand, there is a set of anterior modules, shown in Figure 1, which are particularly active both during the MAE period and just after the cessation of oscillatory movement of the bars both up and down (after which there is no MAE experience reported). Finally there are inferior parietal regions which demonstrate activity almost solely in response to the MAE period.

In all, then, the experimental evidence points most strongly to the siting of awareness in the parietal lobe. It is possible that the superior parietal lobe is essential, as claimed by Milner & Goodale (1995), since the patient DF lost the ability to make actions (involving the superior parietal lobe) in a conscious manner on oriented objects although was able to make the correct actions automatically. However, it may be that such actions involve a 'motor' version of conscious experience, not usually regarded as consciousness. We will not overstep the experimental bounds if we conclude that at least the inferior parietal lobes are essential for consciousness.

Characteristics of consciousness

In this section we give a list of characteristics of neural activity needed for consciousness to be present, together with supporting evidence:

i) Temporal duration. Neuronal activity must be present for at least 0.2s for awareness to arise. This is supported by data of Libet *et al* (1964) and by the duration of activity in buffer working memory sites, suggested by a number of workers as being the sites of creation of consciousness (Taylor 1999).

ii) Competition for consciousness. This is needed for a unique winner to occur, and to help remove ambiguity in interpretations of inputs (Taylor 1996a).

iii) Bodily inputs available. Such inputs are needed to give a perspectival character to inputs, following detailed investigations by psychologists (Bermudez *et al* 1995).

iv) Salience of inputs available. Coded in the limbic system, salience is needed to give a suitable level of importance to a given input. This salience can arise, for example, from the cingulate cortex, as involving motivational activation (Luu *et al* 2000).

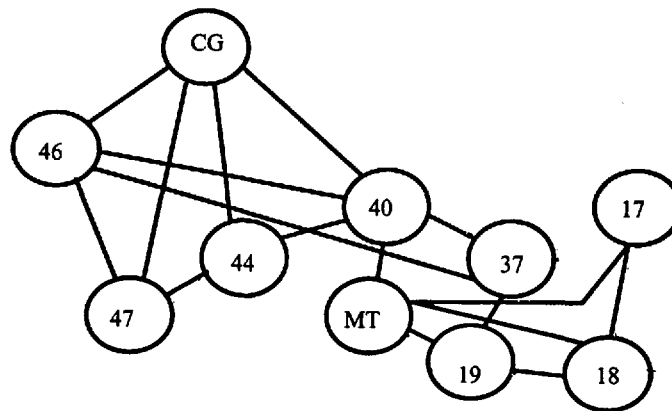v) Past experience. This is making use of previous relevant experience, and arises initially from the hippocampus.

Figure 1   **The network of areas active in the brain during the MAE experiment (Taylor *et al* 2000). The lines joining the various modules denote those for which the correlation coefficient is at least 0.4. MT denotes the middle temporal area, CG the cingulate gyrus, and the other areas are numbered according to Brodmann's numeration (Talairach & Tournoux 1988). The areas 44, 46 and 47 are in the prefrontal cortex, area 40 is in the inferior pariatal lobe, 17 is the primary visual cortex, and 18, 19 and 37 are higher order visual cortices.**

All of these inputs are available, it would seem almost uniquely, for the inferior parietal lobe. Thus the buffer working memory sites for space and time (and language) have been noted as being there (Jonides & Smith 1997; Coull & Nobre 1998), and a competition for consciousness is also associated with these sites (Taylor 1996a). Bodily inputs are also available there, as noted from effects of manipulation of the body in neglect, as well as from known neuroanatomy (connections with the vestibular apparatus and the cerebellum are well known). The limbic system is also well connected to the inferior parietal lobe (Stein 1992) and so is episodic memory. For example, in rats the parietal lobe has been shown to be the final resting place for memories built during step-down inhibition learning (Izquierda *et al* 1997).

Thus we conclude, in support of the conclusion at the end of the previous section, that the inferior parietal lobe (IPL) is suitably connected and structured to satisfy all the above criteria for the creation of consciousness.

The central representation

Evidence from neglect studies and brain imaging on healthy subjects has been presented above to implicate the IPL as playing an important role in controlling attention and awareness. Both of these attributes can occur in a range of possible frames of reference: neglect can be observed tied to an object, or to a trunk-centred frame of reference or a variety of other reference frames (Milner 1997). This implies that the IPL is very likely composed of a set of modules, each carrying information from the environment as well as modulation by possible body input. Thus the IPL is eminently suited to carry what is termed the 'central representation' (CR). This is defined as follows (Taylor in press):

> The central representation is the combined set of multimodal activations involved in fusing sensory activity, body positions, salience and intentionality for future planning; it involves a competitive process between the various modules it contains to single one out to be conscious and be used for report to other working memory sites for further planning or action.

There are several important features of the CR defined above that need discussion, in relation to the criteria of the previous section:

i) The CR must have access to sensory input, such as vision, coded at a high level. Thus, it must have good access to temporal lobe representations, so as to use the categorization built there to guide action.

ii) It must also have access to the bodily input needed to guide actions in terms of the intentionality coded in the superior parietal lobe. It has been noted already that such intentionality is coded for various sorts of actions: of the limbs, eyes, head or fingers (Kalaska *et al* 1997). This intentionality must be furnished with the parameters of the objects on which the actions must be taken; cerebellar and vestibular input also needs to be accessible to the CR, as it is in the parietal lobes.

iii) Salience of inputs in the sensory field is an important attribute for the guidance of actions arising from limbic input already activated to provide saliencies of inputs from the orbitofrontal cortex by way of the cingulate. This is compounded by activations in the retrosplenial (posterior cingulate) gyrus, encoded as parts of episodic memory (Mesulam 1985; Izquierda *et al* 1997). Such connections have been especially emphasized by Mesulam, who wrote, in discussing the important limbic connections to the parietal lobe involved in neglect, that: 'however, the cingulate and retrosplenial projections are much more selective and may be related to more complex and learned aspects of motivation'. Both this and the aspects noted under points i) and ii) above support the IPL as the site for the CR, since it has good connections to the temporal lobe as well as to bodily inputs.

iv) Several modules involved in the CR are found in the IPL; the total activity must undergo an overall competition, possibly aided by thalamo-nucleus reticularis processing. A simulation of such a model has been given earlier (Taylor & Alavi 1995). The existence of such competition is supported by attentional deficits observed in subjects with pulvinar lesions (Posner *et al* 1987).

v) Siting the emergence of awareness in the IPL, as the product of the competition ongoing there, is supported by a simulation of the data of Libet *et al* (1964). This involved the creation of sensory experience (that of a gentle touch on the back of the patient's hand)

by direct stimulation of cortex in patients being operated on for dyskinesia and related movement problems. The simulation (Taylor 1996a) used a simplified model of the cortico-thalamo-nucleus reticularis circuit, and led to the observed dependence of the delay of awareness on the strength of the threshold current for experiencing the touch on the back of the patient's hand.

vi) Such a competition has also been suggested (Taylor 1996b) as occurring to explain experimental results of subliminal effects on lexical decision response times obtained by Marcel (1980). The experiment involved measurement of the reaction times of subjects to deciding if the first or third of three letter strings were words or not. Subliminal exposure to priming words occurred with the second letter string under one condition, with the presentation of polysemous words such as 'palm', on which the lexical decision had to be made to the third word. The prior exposure caused the decision to be speeded up or delayed in characteristic ways according to the semantic relations of the three words to each other; the simulation was able to explain these results by means of a competition assumed to occur on the phonological store, aided and abetted by activations from a semantic memory store.

In conclusion, we site the CR in the IPL as the confluence of information on salience, episodic memory, high level coding of inputs and information on body state.

A model of the emergence of awareness

We are now in a position to put together a framework from which we can understand various processes that are involved in the emergence of awareness of an input. We will again consider here only visual inputs, although there is no reason in principle why the framework does not also apply to other sensory modalities. We will start by considering how to modify the framework of feature integration theory (Treisman 1988) to include the unique role of the CR: feature integration is used here because it forms a useful model incorporating a considerable amount of psychophysical data on vision. It is used here as a plug-in model for the attentional component of the system.

The original model of feature integration assumed that an input was initially encoded on a set of feature maps (for separate colour, texture, motion, etc) and its spatial position on a master 'spatial' map. An 'object file', acting as a temporary object representation, was also set up by the input on a separate module. This object file used spatio-temporal coding as well as other attributes (such as the name) of an object to give it identity. Attention drawn to a particular position on the master spatial map caused correlated activations at the same positions on the feature maps and integrated them together to bind with the activation in the object file.

We extend the above model in terms of a modified version of the feature integration theory presented in Henderson (1994), which includes the manner in which information about objects is stored across saccades (rapid eye movements, made about 3 times a second); it reduces the object files to solely having space-time co-ordinates. This agrees with the conclusions of Pashler (1998) on attentional selection: 'selection by any criterion seems to be ultimately mediated by location selection'. Further information on semantic categories and object models are in quite separate modules in the ventral pathway. This modification is based on numerous psychophysical experiments to assess the level of storage of visual inputs both across saccades and across short delays. The experiments that supported the extension of the feature integration theory used pairs of objects (letters, together with shape distractors) which were either shown at a central visual position within a single eye fixation, viewed

across a saccade movement, or viewed at different retinal and spatial locations over time. Information about the objects was observed to be maintained over time both by episodic object representations (the 'object files') and by long term memory representations (the 'object models'). Neither of these were found to code specifically for sensory information and, as Henderson (1994) wrote: 'object files can be thought of as episodic object tokens that are individuated by spatio-temporal co-ordinates'. Thus the master map of space and the object files are identified in the extended version (Henderson 1994) of feature integration theory.

The use we make here of this model is as follows. Firstly, the spatial nature of the object files supports their being placed in the IPL as part of the CR; involvement of parietal lobe in the process of feature integration had already been suggested by Treisman *et al* (1990). Secondly, and more importantly, the placement of the spatial object files in the CR leads to the proposal that visual awareness arises in the object files map itself. This is through a competition taking place on the CR (Taylor 1999). Thirdly, the sensory components of the object files encoded in earlier visual processing stages are made accessible to awareness, we propose, through feedback coupling to the IPL.

The extension is given in Figure 2, which contains amendments to Figure 7 of Henderson (1994) in terms of the identification of the object files module with the CR and the concomitant competition being carried out there; at the same time we have introduced salience and episodic memory inputs from the limbic system, following the comments of Mesulam (1985) mentioned earlier, and also an input from the superior parietal lobe to include possible intentionalities available to be made on the input. In terms of the original feature integration theory of Treisman (1988), this corresponds to siting the attentional control identically in the object file itself, and identifying them with the master map of locations.
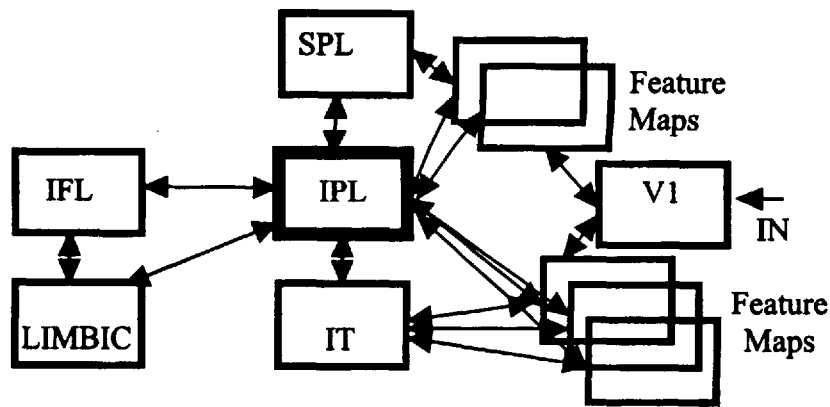

Figure 2   **The updated version of the feature integration theory including the central representation and other supporting modules. SPL = superior parietal lobe, as siting of intentionality; IPL = inferior parietal lobe, as siting of attentional controller and the NCC; IFL = inferior frontal lobe; IT = inferior temporal lobe, as siting of object models.**

We add that the further prefrontal and sensory area contributions to the model of Figure 2, beyond the feature integration theory (Treisman 1988; Henderson 1994) incorporate aspects

from the early and late stage models of the emergence of consciousness (Crick & Koch 1998; Pollen 1999). The various additional modules in Figure 2, beyond the central one of the CR, give the extra contents of consciousness. Thus the process of the development of awareness of an object according to the above model occurs through the following stages:

i)   early visual coding leads to activations of feature representations in V4, MT and similar early visual areas in both the ventral (temporal lobe) and dorsal (posterior parietal lobe) streams;

ii) a set of possible intentions for motor actions on the objects of the visual scene is set up in the superior parietal lobe;

iii) emotional salience and earlier relevant episodic memories associated with the inputs are activated in the limbic system, especially the cingulate and retrosplenial gyrus, by inputs being fed subcortically to the amygdala and hippocampus and so activating the limbic system preconsciously;

iv) object models are also activated at a preconscious level in the temporal lobe on the basis of previously encoded categories;

v)   attentional focus and awareness of the object at the centre of the fovea arises by the process of winning the competition between various activations (object files) still present on IPL in the CR, and those just created by new visual inputs which have just arrived there. These activities consist of representations which are encoded in a spatial form, as is basic to feature integration theory. We show in Figure 3, in schematic form, the resulting set of spatial maps for vision, audition and somatosensation.
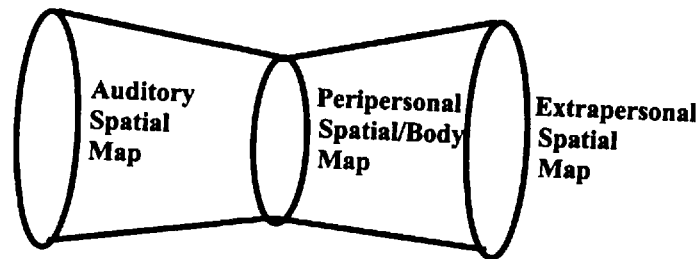

Figure 3   The set of spatial maps as part of the CR. The peripersonal map involves kinetic/visual neurons; that of extrapersonal space is of the usual visual field in trunk-oriented co-ordinates. Finally, the auditory spatial map is correlated with the extrapersonal map.

The intersection regions correspond to the representation of peripersonal space (that around the body). It is possible that there are very few such distinct modules in the central representation: it may even consist of only one such overall, with all the spatial maps fusing into a continuous one, or being several such maps but in register (as for the relation between the extra-personal visual map and the auditory one). Such a restricted number of modules will enable the attentional competition to be run more swiftly and efficiently.

A control approach to the central representation

There has been much development of the 'observer' approach to control modelling to explore the manner in which the brain controls motor actions (Miall & Wolpert 1996). An

observer model is simply an estimator of some plant that has to be controlled but whose states are difficult to observe directly or in a rapid manner. Thus in making an arm movement it takes several hundred milliseconds for proprioceptive feedback to arrive at the central controlling units in the somatosensory/motor cortex. An 'estimator' model of the state of the arm has been suggested by a number of different groups as being created by learning in the brain so as to be able to provide a more rapid control system, and so as to be able to correct errors long before they occur: there is now considerable support for this approach.

Not only are motor actions susceptible to such a control model approach, but so are other forms of action, including language, thinking and planning. The most relevant action for our analysis of consciousness is that of the movement of attention. This is known to be coupled tightly to consciousness, it being necessary for attention to be paid to an object for consciousness to arise of it, as already noted by William James (1950). Attention is also strongly related to the preparation and making of saccades, but can be dissociated from them. One can attend to a different place than where one is fixating, and covert attentional movements are being investigated ever more closely by single cell and brain imaging methods.

Attention is crucial for the creation of unified percepts in which several features represented in different cortical modules are combined, the so-called 'binding problem'. In order to encompass the analysis of visual attention processing in the monitor/observer framework, the notion of the 'movement' of attention will be used: attention is regarded in common speech as an active process.

The various components of an observer model for attentional movement control are specified in Table 1 (Taylor 2000). The first column consists of the functionally-defined modules involved in the movement of visual attention. This is considered as being composed of either an endogenous or an exogenous component: the former of these is controlled by a goal and willed intention system, the latter by a module signalling stimulus intention from external input. The second column is a set of proposed brain areas where the functional modules of the first column are sited.

Table 1 **The observer model of visual attention. The first column consists of the functional modules involved in moving attention, either of an endogenous or exogenous form. The second column is the possible brain sites for the functional modules of column 1. TH = thalamus; NRT = nucleus reticularis thalamus; SEF = supplementary eye fields.**

Attentional system	*Possible brain sites*
Intentional controller of endogenous attention	Anterior cingulate
Endogenous attention observer	Frontal Eye Fields/SEF
Visual state buffer	Posterior parietal lobe
Associative cortical feature modules/object representation modules	Extra-striate occipital and temporal areas
Inverse model action planner	Superior parietal lobe
Monitor	Inferior parietal lobe/NRT/TH
Exogenous attention controller	Superior colliculus

The basis of the model of attention subsuming Table 1 is that of feedback amplification of target activity and inhibition of non-target activity, from the higher-order attentional action map (the inverse model action planner module of column 1), onto activity on a set of feature maps (coding for colour, motion, shape, etc), each having a topographical representation of the visual input. The amplification/inhibition can be by modulation with lateral inhibition (Taylor 1996a), or by direct excitation/inhibition of feedback activity to that at the lower level modules. There is a competitive process on the action planner map, in which there is also a contribution from the endogenous and exogenous intention modules (which are also topographic maps). Finally, there is a monitor for assessing the error in the amount of attentional movement achieved as compared to what has been desired (as signalled from the inverse model controller). This also plays a crucial role in updating the state estimate (the observer state). Without it, the estimate of the state will become different from the real state value so that new action commands will develop errors.

The nature of visual attention, as encapsulated in the second column of Table 1, is consistent with experimental observations. Thus visual attention has a strong spatial localization (Pashler 1998), so that the attention action planning module is supported as being a location to which the focus of visual attention will next move. The controlling module involving sudden external inputs is now generally regarded as being the superior colliculus. There is increasing support from brain imaging that the network of controlling modules for top-down control of visual attention includes the anterior cingulate, the frontal eye fields and the parietal lobes, as well as some involvement of the prefrontal cortex (Coull & Nobre 1998). The anterior cingulate has been suggested as being involved in motivation, the frontal eye fields in willed intention, while the posterior parietal component is suggested as being concerned with coding of intentions. The monitor is noted as being in the parietal lobes; its presence in the inferior parietal is indicated by neglect. Therefore, the assignments of Table 1 have support. Finally, modelling of a portion of the model (Mozer & Sitton 1997) indicates that more detailed neural implementation agrees with a range of psychophysical results on attention processing. The monitor component of the model, identified with the cortical-thalamo-nucleus reticularis thalami (NRT) system, has been noted earlier to fit known data (Taylor 1996a, b).

Animal welfare implications

The above model of consciousness being created in the CR, acting as part of an attentional control system, has been based not only on human data but also on a considerable amount of data taken from primates (mainly monkeys). Thus the question of animal consciousness, of crucial concern for animal welfare, has already been considered at the primate level: such animals would be expected to possess at least primary (non-reflexive) consciousness. The question as to how far down the evolutionary scale such consciousness occurs may now be tackled in a preliminary fashion in terms of the above overall model.

In summary, the model proposes that consciousness is created in the CR in the parietal lobes, in which are sited various components of the overall control mechanism for attentional movement control. These include an inverse model controller, a monitor and a working memory buffer. The monitor is involved in attentional disengagement, shifting and re-engagement, at the heart of attentional movement. These processes are thought to be carried out by the thalamus-cortex-NRT complex, which has been modelled by a number of groups. Recent evidence in support of the claim that the NRT is important for the movement of attention has come from important work on the effect of one-sided destruction of the NRT in rats (Weese et al 1999). This has shown that covert attention is ineffective in speeding up

response to inputs arriving on the contralesional side; priming in otherwise healthy NRT, for which a speed-up is known to occur, does not do so in the damaged case. This indicates that in the rat there is a contribution to covert attention movement by the system that is also claimed by a number of researchers to be used in humans. There is also evidence, noted earlier (Izquierda *et al* 1997) that parietal cortex is an important site of learning of control for avoidance behaviour in rats. Thus it would appear that a number of the sites recognized as crucial for attentional movement in humans are also functioning in a similar manner in the rat. It is to be expected that the rat, and animals of a similar brain structure, will experience non-reflexive consciousness.

An important question for animal welfare is that of the experience of pain. Given that the rat can phenomenologically experience visual and other inputs, as indicated by the above discussion, what will its experience of pain be? This is a very difficult question, given that there is still considerable controversy as to the neural basis of pain experience in humans. I will extend the above attentional movement control model of consciousness by suggesting that pain is brought about by its activations, in insula, SII and anterior cingulate, trapping attention from moving to other targets. In particular, the anterior cingulate is known to be an important component of the attentional circuit, so that cingulate pain activation will enter this circuit and prevent further attentional movement to other desired inputs. This will lead to the phenomenal experience of pain as an undesirable attractor, reducible if attention can be attracted away from the pain signal (as is known in cases of severe injury on a battlefield where higher concerns arise initially). A similar attention-based model of pain should apply to other animals for which there is an attentional control system able to support conscious experience.

Discussion

Our first conclusion is that the parietal lobes are the essential site in the brain for animal consciousness. We emphasize the crucial feature of the CR, based there, in comparison to feature integration theories (Treisman 1988; Henderson 1994). Awareness of an input arises by its representation on the object file/attentional map/CR winning the competition there. This leads in general to identification of initial awareness of an input with its 'token', as a specific object, not its 'type' or category. The identification of the type of an input will be expected to take longer, since there has to be conjoint activation of the object model module with the CR, and then resulting activation of the relevant working memory. Similar object-specific coupling to the sensory feature maps must also be enhanced.

Secondly, the CR was then unpacked a little by means of a control approach to the movement of attention. This depended on the presence of neuronal systems able to generate a control movement, as well as a monitor of the effectiveness of the resulting control signal. This latter was also used to update, very likely in the frontal lobes, an observer model of the attentional state of the system by means of an error signal. This control structure was suggested as being necessary in order that non-reflexive consciousness could arise.

The third conclusion is that absence of the relevant neuronal structures needed to support attention movement would indicate that there would be no reason for expecting there to be any conscious experience. At the level of the rat, such structures were found to be active and therefore consciousness was very likely able to be created in such animals. However, this conclusion needs more careful analysis in order to ensure that the neural systems present are actually able to perform the attentional control functions known to be present in humans. Pain was a specific experience suggested as being able to be present if the attentional control

system was intact. Extension of the consciousness model to lower animals is of great relevance but has not yet been performed.

Finally, the nature of higher reflexive consciousness will depend on further control structures able to support the attending of attention to itself. The possibility of possession of enough cortex for that can be questioned for the monkey (Milner 1997), where the homology of the inferior parietal lobes between human and monkey is still uncertain. It is reasonable to suspect that enough cortex is needed to support mirror self recognition; that does not occur for the monkey.

All of these aspects are of the deepest importance for animal welfare. In all, the control systems approach to high level cognitive processes should enable real scientific progress to be made on the deep but important questions of the nature of animal consciousness. This should therefore be of prime concern to all who wish to reduce unnecessary suffering in animals.

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